

The University of Chicago

ROOT-STEM TRANSITION
OF OPUNTIA ENGELMANNII
SALM-DYCK

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1937

By

WILLIAM MAYNE LONGNECKER

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INTRODUCTION

As a result of a wide interest in the Cactaceae, because of their cosmopolitan distribution and varied growth habits, a voluminous literature concerning them has appeared, the bulk of it consisting of treatises on taxonomy and of various semipopular writings. Among the articles more pertinent to the subject here discussed, Lubbock (4) has described the seeds and seedlings of several species, his figures of the seed of Opuntia dillenii being similar to that of O. engelmannii. Engelmann (1) published excellent figures, including some of seeds and embryos, but these were mostly of the melon forms, as *Ferocactus*. Labouret (3) briefly described the germination of several species. Numerous authors, including Ganong (2), Solereder (7), Preston (5), and others have written on the anatomy of the mature stem, and there are innumerable publications on special structures, as hypodermis, crystals, cutin, and spines.

Opuntia engelmannii Salm-Dyck, one of the prickly pear cacti, occurs in western Texas, New Mexico, Arizona, and adjacent provinces of Mexico. Shreve (6) characterizes this species as the "king of the opuntias," because of its ". . . large joints, erect and spreading limbs, long white spines, magnificent yellow flowers."

METHODS AND MATERIALS

Seeds were collected in Jeff Davis County, Texas, in the autumns of 1934 and 1936 and seedlings were grown from them in the greenhouses of the University of Chicago. These were killed and fixed at ages varying from one day to three weeks. A variety of fixatives was used, none being entirely satisfactory. Nawaschin's solution and Crooks' modification of it were most successful. Sections were cut at 8 and 15 microns. Drawings were made with a microprojector.

FRUIT AND SEEDS

The fruit of this species is ovoid and reddish-purple when mature. It is 3.5-5 cm. long and 2-3 cm. in diameter. At

its distal end a concavity about one centimeter in diameter and 2-4 mm. in depth marks the former position of perianth, stamens, and stigma. The several parietal placentae, enlarged inwardly, form a pulpy interior in which more than 100 seeds frequently develop from campylotropous ovules. Seeds are flattened, with irregular faces, 3.5-4.5 mm. long and slightly more than 1 mm. in thickness. In face view they are oval or reniform. A thick, bony testa, composed of circularly and transversely interwoven fibers, surrounds the embryo, and forms a heavy marginal ridge which encircles the remainder of the seed. A thinner submarginal ridge is present on each face. The tegmen is thin and is dark brown in color, in contrast with the paler, almost flesh-colored testa. The embryo is curved, the cotyledons lying at an angle of about 90° with the hypocotyl, and their tips recurved. The greater part of the scanty endosperm lies in the curve of the embryo, and the remainder extends to the tip of the radicle.

GERMINATION

Under greenhouse conditions seeds germinated most commonly in 8-21 days. Of the first seeds planted only a small percentage germinated, and various treatments, including freezing, scarification, and soaking in ether, were tried. All increased the percentage of germination considerably, the ether treatment proving most effective. In seeds planted the second year after collection, germination of untreated seeds was fairly high (68%) suggesting a possible need for a period of after-ripening. Polyembryony was frequent, more than 20% of the seeds giving rise to two, rarely three, seedlings. Fasciation in varying degrees occurred occasionally.

In seedlings a day after they have broken through the soil, the outer and longer cotyledon is 5-7 mm. in length, the inner one being 1-2 mm. shorter. The hypocotyl is 7-8 mm. long, and the primary root may extend for a centimeter or more into the ground. The epicotyl is scarcely visible at this age, but 5-10 days later numerous hairlike outgrowths may be noticed between the cotyledons, and the young stem gradually enlarges, appearing at the end of a month as a spiny, more or less hemispherical protuberance, 2-3 mm. in diameter. It bears numerous subulate leaves, arranged spirally, as well as many small spines. Under greenhouse conditions the cotyledons remain attached for two months

or more, gradually shrivelling from their apices backward before their fall.

At the cotyledonary node a tiny bud may be discerned microscopically in the axil of each cotyledon. In plants three days old these buds are only 75 microns in diameter, and are pointed apically. Only four or five layers of cells separate them from the principal cotyledonary bundles, although no vascular connection is apparent at this age. Lateral to each bud several multicellular hairs with somewhat flattened bases may be seen. The buds, and sometime the apical meristem of the epicotyl, may contain crystals, presumably of calcium oxalate. Those observed varied from 15-30 microns in greater dimension, were drusiform, and a single large one frequently filled a cell cavity. Ganong (2) and Solereder (7), as well as other writers, refer to the presence of such crystals in the hypodermis of other species of *Opuntia*, but make no reference to their occurrence in seedlings.

HYPOCOTYL AND TRANSITION

The hypocotyl is about eight millimeters long, but the transition is largely confined to its upper fourth. Up to about two millimeters below the cotyledonary node it is essentially rootlike in structure, except that its center is parenchymatous. At lower levels it possesses four protoxylem points, each consisting of two or three spiral, or more rarely, annular elements. Four protophloem groups alternate with the xylem, and one, or sometimes two pericyclic layers enclose these and the contained pith, forming a stele which is roughly square. Endodermal and other cortical cells are much larger than those of the pericycle. Casparian strips are discernible in the lowest two or three millimeters of the hypocotyl. The cortex consists of from six to ten layers of cells, the number increasing somewhat at higher levels. Collenchymatous cells are absent from the other layers and there is no clearly defined hypodermis. Only about a fifth of the diameter of the hypocotyl is composed of stelar tissue.

A section taken at a level five to six millimeters below the epicotyl appears as described in the preceding paragraph (Plate I, fig. A). Sections at successively higher levels for about three millimeter show only one major change: the number of protoxylem elements at two alternate points comes to be reduced as parenchymatous cells are differentiated in their places and

presently one point (Plate I, Fig. B), then the other (Plate I, fig. C) disappears. As a result of this differentiation of parenchyma rather than xylem, a section at a level 1.5-3 mm. below the epicotyl shows the developing vascular system to consist of two protoxylem points, each one lying between two protophloem groups.

One or two metaxylem cells are commonly differentiated centrad to the two active protoxylem points, and one or more than arise lateral to either the protoxylem or the newly formed radial metaxylem (Plate I, Fig. C). These last differentiated metaxylem cells occur laterally, toward the protophloem, forming an irregular line of primary xylem, extending from near the inner surface of one protophloem group to that of the other (Plate I, Fig. D). In plants more than a day or two old, early secondary growth may be seen centrad to the protophloem, and secondary xylem is differentiated near the last formed metaxylem.

While these changes in the development of the xylem are going on, a change in the position of the protophloem occurs. At the lower levels first described the phloem is radial. At about one and a half millimeters below the cotyledonary node the innermost cells of the protophloem are developed slightly nearer the xylem. At successively higher levels this shift becomes more marked until at a level about a half millimeter below the node the horizontal axes of two of the protophloem groups are almost in line with the included primary xylem, the two opposite phloem groups bearing a similar relation to the other xylem point (Plate II, Fig. A). Each such grouping of vascular tissue becomes a cotyledonary bundle.

As these bundles diverge about 30° from the vertical and extend into the cotyledons, the primary xylem usually develops as three groups, each group consisting of a few conducting elements, separated from the others by intervening parenchymatous cells. The two outer groups are of two to four metaxylem elements, the inner one of protoxylem. Distinction between the elements is difficult, since nearly all possess spiral thickenings. Serial sections from the base of the cotyledon show that these xylem groups tend to be differentiated more and more closely together, the four or five protoxylem elements coming to develop ventral to the metaxylem. As this change in relative position of the xylem takes place, the two phloem groups of the trace tend to be differentiated

more and more nearly dorsally with respect to the xylem, and closer and closer together, with the result that at their convergence, about a millimeter beyond the cotyledonary node, the bundle is endarch collateral (Plate II, Fig. C).

At the cotyledonary node vascular extensions into the epicotyl become evident. In sections of a plant three days old, cells of the protophloem are scarcely distinguishable from the provascular strands, cells of which occur adjacent to the protophloem and apparently continuous with it. From the provascular cells adjacent to each of the four protophloem groups, a provascular strand extends centrad and upward into the epicotyl. A section just above the cotyledonary node shows four such strands (Plate II, Fig. B). The strands extending from opposite phloem groups develop closer and closer together at higher levels, and presently converge about 100 microns above the level at which they first become visible. From near the apex of each of the arch-like structures of provascular tissue thus formed a single strand extends upward and laterally, one to the first, the other to the second true leaf.

At a level about 100 microns higher another group of four provascular strands extends from points adjacent to the four protophloem groups which are slightly diverged into the bases of the cotyledons at this level. These also develop centrad and upward. Two strands, almost diametrically opposite each other, are differentiated into two branches each, which extend into later developing leaves. The other two extend upward and anastomose with the strands to the first leaves mentioned (Plate II, Fig. C). With later stem development new provascular strands differentiate as extensions and ramifications of the eight principal strands mentioned.

SUMMARY

1. The fruit, seed, and seedling of Opuntia engelmannii Salm-Dyck are described.
2. In the lower part of the hypocotyl four protoxylem points are differentiated. At higher levels two of these fail to differentiate.
3. At the base of each cotyledon the principal cotyledonary bundle consists of two protophloem groups, between which lie three parallel strands of primary xylem. The central one is

of protoxylem, the outer ones metaxylem. At higher levels in the cotyledon the protophloem groups develop more dorsally and closer together, becoming adjacent and the metaxylem is differentiated ventral to them. Protoxylem comes to be differentiated ventral to the metaxylem, the relative change in position of these tissues giving rise to an endarch collateral bundle.

4. Vascular connections between hypocotyl and epicotyl consist of eight provascular strands extending from a position adjacent to the protophloem into the epicotyl.

Acknowledgment

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EXPLANATION OF PLATES

Plate I

Figs. A, B, C. Transverse sections of hypocotyl at levels of 5, 3.5 and 2.5 mm. below cotyledonary node, respectively, showing four, three, and two protoxylem points.

Fig. D. Transverse section of hypocotyl 2 mm. below cotyledonary node, showing arrangement of metaxylem.

px, protoxylem; mx, metaxylem; pph, proto-phloem; pc, pericycle; pi, pith.

Plate II

Fig. A. Transverse section of hypocotyl 1 mm. below cotyledonary node, showing position of protophloem.

Fig. B. Transverse section through cotyledonary node.

Fig. C. Schematic diagram of vascular tissue adjacent to the cotyledonary node.

px, protoxylem; pph, protophloem; pv s', provascular strand to first leaf; pv s", provascular strand to second leaf; mx, metaxylem; cot bu, cotyledonary bundle.

PLATE I

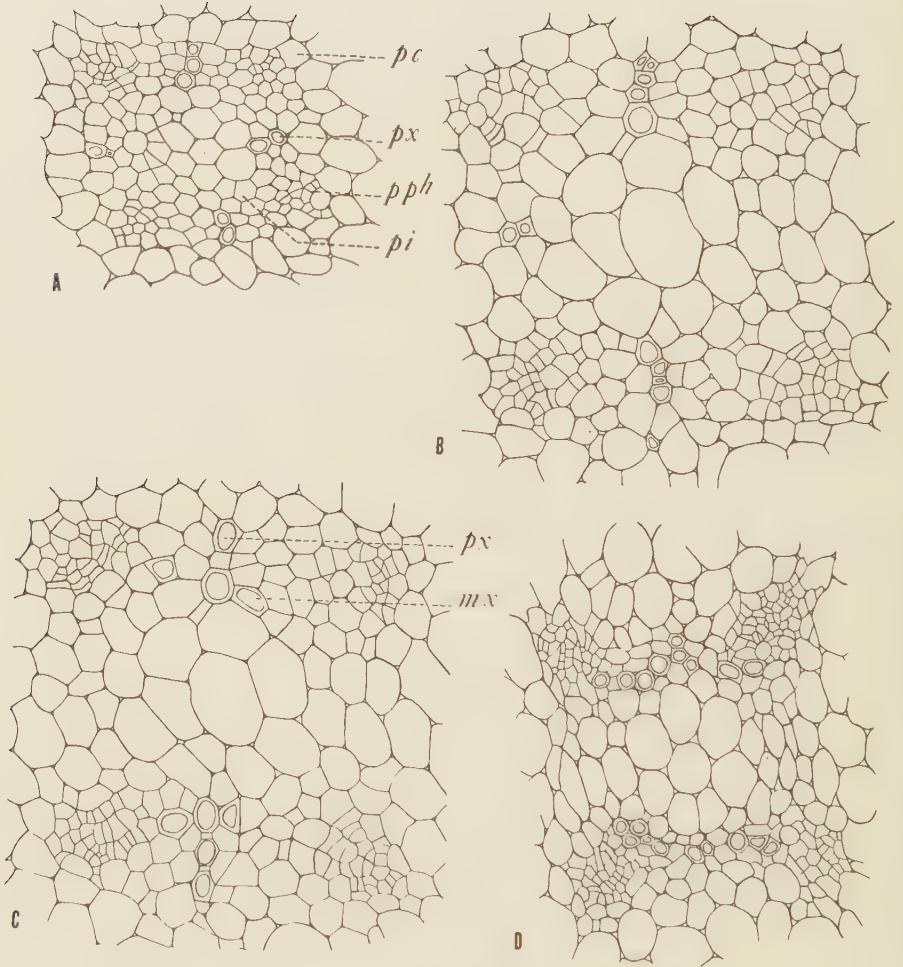


PLATE II

